HACKELIA TAYLORI (BORAGINACEAE), A NEW SPECIES FROM NORTH CENTRAL WASHINGTON STATE (U.S.A.)

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ABSTRACT

Hackelia taylori (Boraginaceae), here named, is known from only three populations. Plants are found growing on very steep, sandy/gravelly talus slopes within the Alpine Lakes Wilderness, Okanogan-Wenatchee National Forest, Washington, USA. The species differs from similar *Hackelia* spp. by having relatively small blue flowers (mean limb width 1.3 cm) with small fornices (mean 0.81 mm), short stature (mean 14.9 cm), short but wide lower cauline leaves (mean length 1.5 cm, width 0.7 cm), and small nutlets (mean length 2.6 mm). Additionally, *H. taylori* is distinguished from the most closely related *H. venusta* by markedly different habitats, different flower color and other morphological characters (cauline leaves, nutlet size, floral structures) which are generally smaller, and lack of seeds produced in controlled crosses.

RESUMEN

Hackelia taylori (Boraginaceae), nombrada aquí, es conocida sólo en tres poblaciones. Las plantas se encuentran creciendo en taludes muy empinados, de arena / grava en las laderas del desierto Alpine Lakes, Okanogan-Wenatchee bosques nacionales. La especie difiere de otras *Hackelia* similares por tener flores pequeñas azules con fondos de saco pequeño, baja estatura, hojas caulinares cortas pero anchas, y núculas pequeñas. Además, *H. taylori* se distingue de la más estrechamente relacionada con *H. venusta* por sus hábitats muy diferentes, ausencia de formas intermedias naturales y la falta de semillas producidas en los cruzamientos controlados.

Hackelia Opiz. includes 45 species of perennial plants distributed within Northern Temperate region, Central and South America combined (Mabberley 1987). In North America, 28 species are recognized, comprising 34 taxa, many of which are narrow endemics (Gentry & Carr 1976). Species of *Hackelia* can be found in a wide range of habitats, including sagebrush steppe, steep talus slopes, moist rock crevices, open deciduous forests, and *Abies* or *Pinus* forests; and the distribution of many species are narrowly restricted based on habitat, geography, or elevation (Carr 1974; Gentry & Carr 1976). Gentry and Carr (1976) completed a comprehensive study of *Hackelia* and clarified taxonomic relationships of the species and subspecies in North America. However, the taxonomic status of *H. venusta* (Piper) St. John has remained in question (Gamon 1988) and recently has been the focus of taxonomic research (Harrod et al. 1999; Hipkins et al. 2003).

Hackelia venusta, as originally described, includes a white-flowered form found at one low elevation site (488 m) 9.6 km northwest of Leavenworth, Washington, and a blue-flowered form found at four currently known high elevation (ca. 2050 m) alpine locations about 18 km northwest and southwest of Leavenworth, Washington (Carr 1974; Gentry & Carr 1976; Hitchcock et al. 1959) (Fig. 1). The two forms were shown to be distinct from each other based on morphological traits (Harrod et al. 1999). However, enzyme band pattern analyses did not provide evidence for taxonomic separation of the two color forms (Hipkins et al. 2003). Although at first this may seem to be a dilemma, taxonomy is often the result of synthesis across many lines of evidence, some of which may fail to support the taxonomic hypothesis (Grant 1992; Winston 1999; Hipkins et

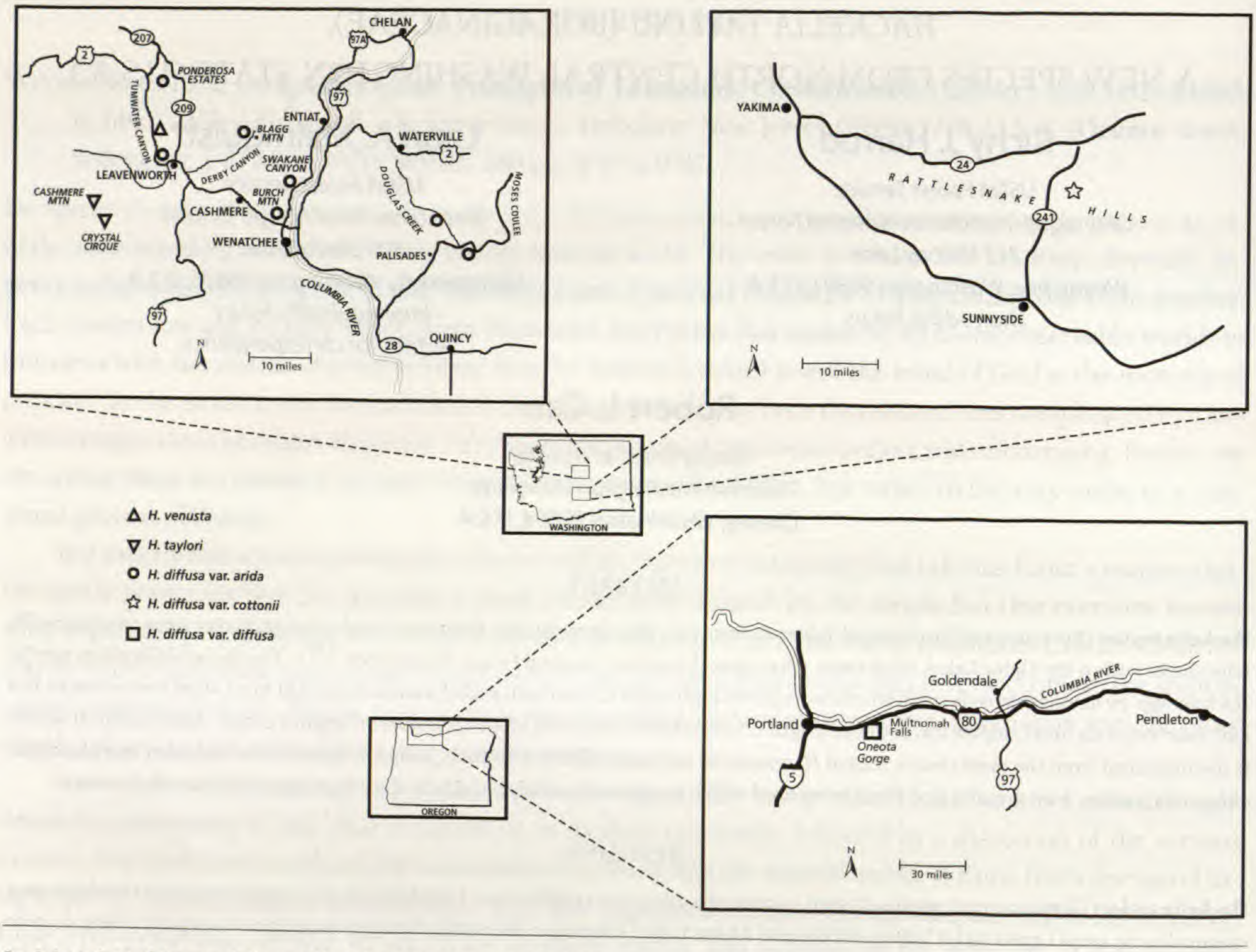

Fig. 1. Locations of the populations of *Hackelia* in Washington State, USA, examined in this study.

al. 2003). Taxonomic entities are defined on a combination of morphology, genotypic data (e.g., isozymes), ecology, reproductive isolation, and geographic distribution. There are compelling reasons to consider the two flower color forms to be separate species based on morphological and ecological distinctions.

Here we provide a technical description for the alpine form at the rank of species, here named *Hackelia taylori*. Although *H. taylori* was shown to be morphologically distinct from *H. venusta* in our previous work (Harrod et al. 1999), we wanted to evaluate the morphological distinctiveness of *H. taylori* with respect to other varieties of *H. diffusa* (Doug. ex Lehmann) Johnston which we did not study previously, but which were included in the enzyme work of Hipkins et al. (2003).

MATERIALS AND METHODS

Study Sites

Data were collected from 10 populations used by Harrod et al. (1999) with 2 additional *H. diffusa* populations that we felt may have some affinity to *H. taylori* (Fig. 1) based on suggestions in Gentry and Carr (1976). The collection site for these two additional sites are: 1) *H. diffusa* var. *cottonii* (Piper) Carr, located on private land in the Rattlesnake Hills (RH), 25 km north of Sunnyside, WA 150 m elevation; and 2) *H. diffusa* var. *diffusa*, located at Oneota Gorge (OG) near Multnomah Falls, 50 km east of Portland, OR 75 m elevation.

Voucher specimens deposited at the Wenatchee River Ranger District herbarium:
Hackelia diffusa var. ***diffusa*****. OREGON. Multnomah Co.:** Oneota Gorge, 52.9 km E of Portland, Harrod 406.
Hackelia diffusa var. ***arida*****. WASHINGTON. Chelan Co.:** Tumwater Canyon, 1.6 km W of Leavenworth, 28 May 1996, *Malmquist 01*; 1.6 km W of Leavenworth, 05 Jun 1996, *Malmquist 02*; Derby Canyon, 11.3 km SE of Leavenworth, 09 May 1996, *Malmquist 05*; 11.3 km SE of Leavenworth, 09 May 1996, *Malmquist 06*; 11.3 km SE of Leavenworth, 09 May 1996, *Malmquist 07*; Ponderosa Estates, 17.7 km N of Leavenworth,

20 May 1997, *Malmquist 08*. **Douglas Co.:** Moses Coulee, 24.0 km N of Quincy, 08 May 1996, *Malmquist 03*; 24.0 km N of Quincy, 08 May 1996, *Malmquist 04*.
Hackelia diffusa var. ***cottonii*. Yakima Co.:** Rattlesnake Hills, 25 km N of Sunnyside, 24 Jun 1997, *Malmquist 09*; 25 km N of Sunnyside, 24 Jun 1997, *Malmquist 10*.
***Hackelia venusta*. Chelan Co.:** Tumwater Canyon, 9.6 km W of Leavenworth, 25 Jun 1991, *Harrod 293*.
***Hackelia taylori*. Chelan Co.:** Cashmere Mountain, 19.0 km SW of Leavenworth, 4 Aug 1996, *Kuhlmann 01*; 16.0 km SW of Leavenworth, 21 Aug 1997, *Benson 01*.

Voucher specimens deposited at WTU:
***Hackelia venusta*. Chelan Co.:** Tumwater Canyon, 9.6 km W of Leavenworth, 31 Jun 1998, *Harrod 410*.
***Hackelia taylori*. Chelan Co.:** Crystal Creek, 19.0 km SW of Leavenworth, 29 Jul 1991, *Harrod 238*; Cashmere Mountain, 16.0 km SW of Leavenworth, 21 Aug 1997, *Benson 02*.

Morphological Measurements and Statistical Analyses

We followed the same methods and used most of the same data (individual plants from original 10 populations with missing morphological data were dropped from analysis) as described in Harrod et al. (1999). Nineteen morphological characters from three categories (vegetative, floral, and fruit) were scored for statistical analysis and an additional 11 descriptive characters (e.g., leaf shape, leaf surface, color) were recorded (Table 1). These data were collected from 25 randomly selected individuals from each population except the Cashmere Mountain population, which consisted of data from 14 individuals, and Crystal Cirque with only 10 individuals. Both principal components and discriminant analyses were performed on the quantitative morphological data using SPSS 16.0 (SPSS, Chicago, Illinois). Principal components analysis (PCA) was used to evaluate the natural groupings among each sampling unit or operational taxonomic unit (population). Discriminant analysis was used to establish the non-arbitrariness of group assignments. This analysis places each case (plant) within the group (population) with which it shares discriminating characters (Anderson and Taylor 1983). The analysis is biased in that it positions cases within the ordination based on discriminating characters to achieve maximum separation of the defined groups. A plot of the cases based on the first two discriminating functions can assist in visualizing distinction among groups and species. The data for these analyses involved a 237 × 19 character matrix.

Descriptive characters were not subjected to statistical analyses but were used to further detail morphological characteristics of the new taxon.

RESULTS

The addition of *H. diffusa* var. *cottonii* and *H. diffusa* var. *diffusa* in both the principal components and discriminant analyses lead to tighter groupings of cases as compared to the results of Harrod et al. (1999). Of the 19 components that accounted for all the variance in the PCA, the first three accounted for 65.1% (32.5%, 20.7%, and 11.9%, respectively). Characters highly correlated with the first component were lower cauline leaf width and length, upper cauline leaf width, and radical leaf width (Table 2). *Hackelia diffusa* var. *cottonii* and *H. diffusa* var. *diffusa* separated from other taxa along the first component (Fig. 2A). Plant height, radical leaf petiole length, radical leaf length, and upper cauline leaf length were characters highly correlated with the second component (Table 2). Along this second component, *H. taylori* (CC and CM) separated from the *H. diffusa* var. *arida* populations forming a distinct group that was somewhat overlapping with the *H. venusta* population (TC) (Fig. 2A). The third component separated *H. venusta* from *H. taylori* and characters highly correlated with the third component were upper cauline leaf length, limb width, fornice protuberance, and calyx length (Table 2, Fig. 2B).

The discriminant analysis showed *H. taylori* was more clearly distinct from *H. venusta* and almost the entire *H. diffusa* complex (Fig. 3). The first two discriminant functions accounted for 81.8% of the ability to distinguish among groups (51.2% and 30.6%, respectively). Total predictability that a case from a certain population was correctly classified to that population was 95.8%. Individual cases (plants) had high predicted group membership with the sampled population from which they were sampled. *Hackelia taylori* plants from CM were 100% correctly classified and those from CC were 95.8% correctly classified, with 4.2% classifying with

TABLE 1. Morphological characters used in the taximetric analysis of *H. taylori* and other *Hackelia* species. All measurements in mm unless otherwise noted.

Vegetative	Floral	Fruit
Plant height (dm)	Pedicel length	Nutlet shape (descriptive)
Radial leaf length	Calyx length	Nutlet surface (descriptive)
Radial leaf width	Calyx shape (descriptive)	Nutlet length
Radial leaf petiole length	Limb width	Number of intramarginal prickles
Radial leaf shape (descriptive)	Corolla color (descriptive)	Flange width
Radial leaf surface (descriptive)	Anther length	Distinct prickle length
Lower cauline leaf length	Fornice color (descriptive)	Fraction connate
Lower cauline leaf width	Fornice appendage height	
Lower cauline leaf shape (descriptive)	Fornice protuberance length	
Lower cauline leaf surface (descriptive)		
Upper cauline leaf length		
Upper cauline leaf width		
Upper cauline leaf shape (descriptive)		
Upper cauline leaf surface (descriptive)		

TABLE 2. Variables used in the PCA and loadings on the first three principal components. The asterisk reflects the top four values for each axis and identifies the variables contributing the most.

Variables	Loadings		
	Axis 1	Axis 2	Axis 3
Lower cauline leaf width	0.904*	-0.029	-0.039
Lower cauline leaf length	0.805*	0.431	-0.019
Upper cauline leaf width	0.800*	-0.140	0.106
Radial leaf width	0.773*	-0.067	0.155
Fraction connate (fruit)	-0.741	-0.304	0.407
Flange width (fruit)	-0.737	-0.251	0.309
Distinct prickle length (fruit)	0.632	0.198	-0.159
Plant height	0.205	0.836*	-0.092
Radial leaf petiole length	0.254	0.793*	-0.178
Radial leaf length	0.228	0.732*	-0.283
Upper cauline leaf length	-0.382	0.717*	0.169
Limb width (floral)	0.028	-0.442	0.800*
Fornice protuberance (fruit)	-0.143	-0.326	0.745*
Calyx length (floral)	0.034	-0.439	0.743*
Fornice appendage (fruit)	0.120	-0.644	0.670*
Pedicel length (floral)	-0.360	0.144	0.646
Nutlet length (fruit)	-0.047	0.329	0.525
# of intramarginal prickles (fruit)	0.231	0.155	0.506
Anther length (floral)	0.008	-0.016	-0.008

CM. The most important characters for achieving separation in this analysis are displayed in Table 3. In the first discriminant function, flange width, calyx length, fornice appendage, and limb width were important discriminating characters. Additionally, fornice protuberance, upper cauline leaf length, lower cauline leaf width, and nutlet length were important discriminating characters in functions 2 and 3 (Table 3).

TAXONOMIC TREATMENT

Hackelia taylori Harrod, Malmquist & Carr, sp. nov. (**Fig. 3**). TYPE: UNITED STATES. WASHINGTON: Chelan Co.: Upper levels of Crystal Creek cirque, ca. 150 m S of Crystal Lake on steep SSE facing slope, ca. 47°28.30'N, 120°48.00'W, 29 Jul 1991, *R.J. Harrod* 238 (HOLOTYPE: WTU!; ISOTYPES: WTU!).

Hackelia venustae (Piper) St. John aspectibus mophologiae ac habitudo similis sed distinctus habitatione locorum editiorum, statura breviore (1–2 dm vs. 2–4 dm), corollis caeruleis (vs. praecipue albas) limbis multo angustioribus (10–15 mm latis vs. 18–22 mm) et fornicibus minoribus (appendix 0.8–1.0 mm alta vs. 1.0–1.4 mm; protuberatio 0.6–1.0 mm longa vs. 1.2–1.8 mm).

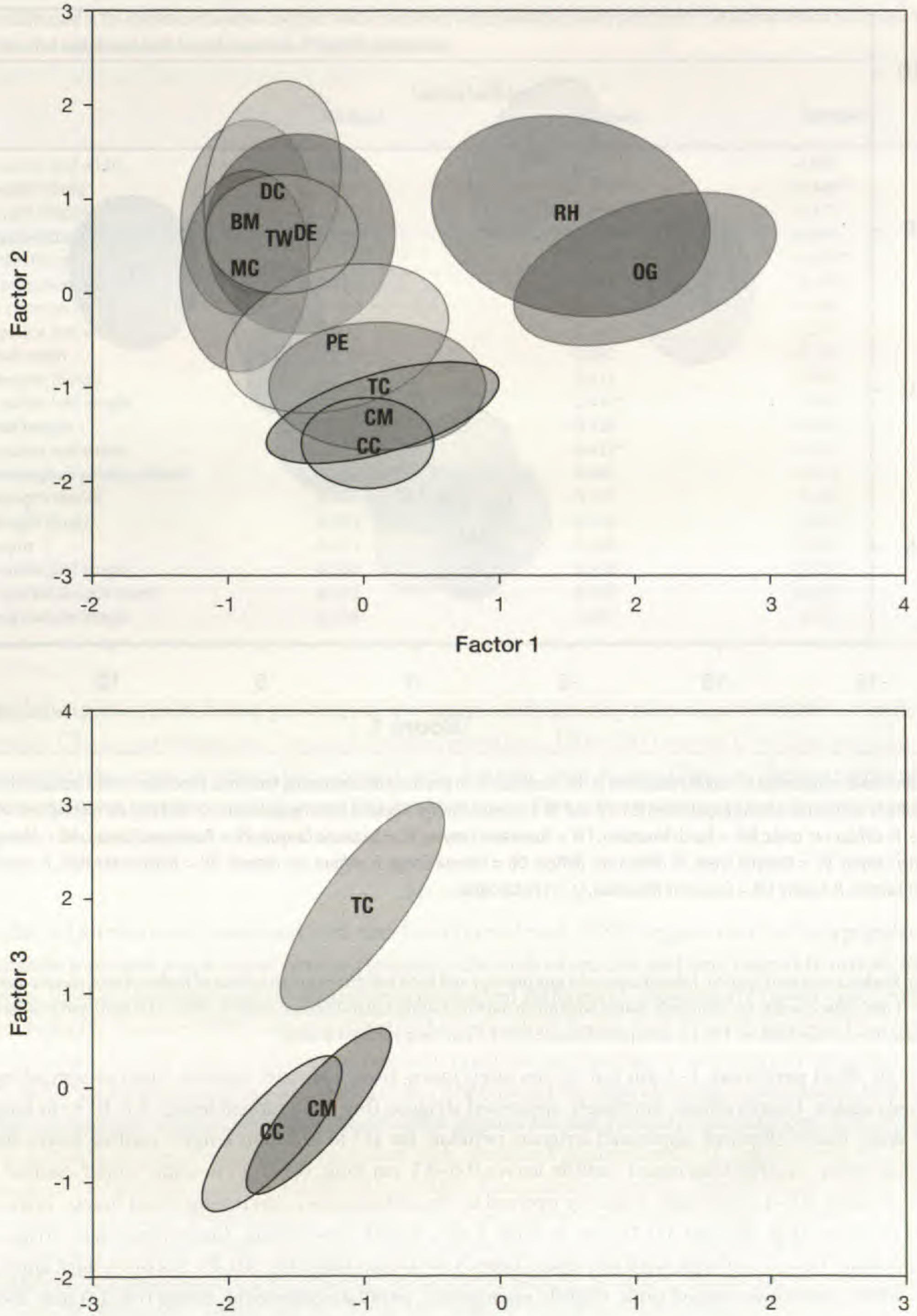

FIG. 2. **A.** Ordination of populations of *Hackelia* examined in this study based on scores of principal components 1 and 2. The first two components accounted for 53.2% of the total variance, 32.5% and 20.7%, respectively. *Hackelia taylori* populations (CC and CM) are highlighted with heavy black line. **B.** Ordination of populations of *Hackelia venusta* and *H. taylori* examined in this study based on scores of principal components 2 and 3. The third component accounted for an additional 11.9% of the variance for a total of 65.1% for the first three. *H. diffusa* var. *arida*: BM = Burch Mountain, TW = Tumwater Canyon, SC = Swakane Canyon, PE = Ponderosa Estates, MC = Moses Coulee, DE = Derby Canyon, DC = Douglas Creek. *H. diffusa* var. *diffusa*: OG = Oneota Gorge. *H. diffusa* var. *cottonii*: RH = Rattlesnake Hills. *H. venusta*: TC = Tumwater Canyon. *H. taylori*: CM = Cashmere Mountain, CC = Crystal Creek.

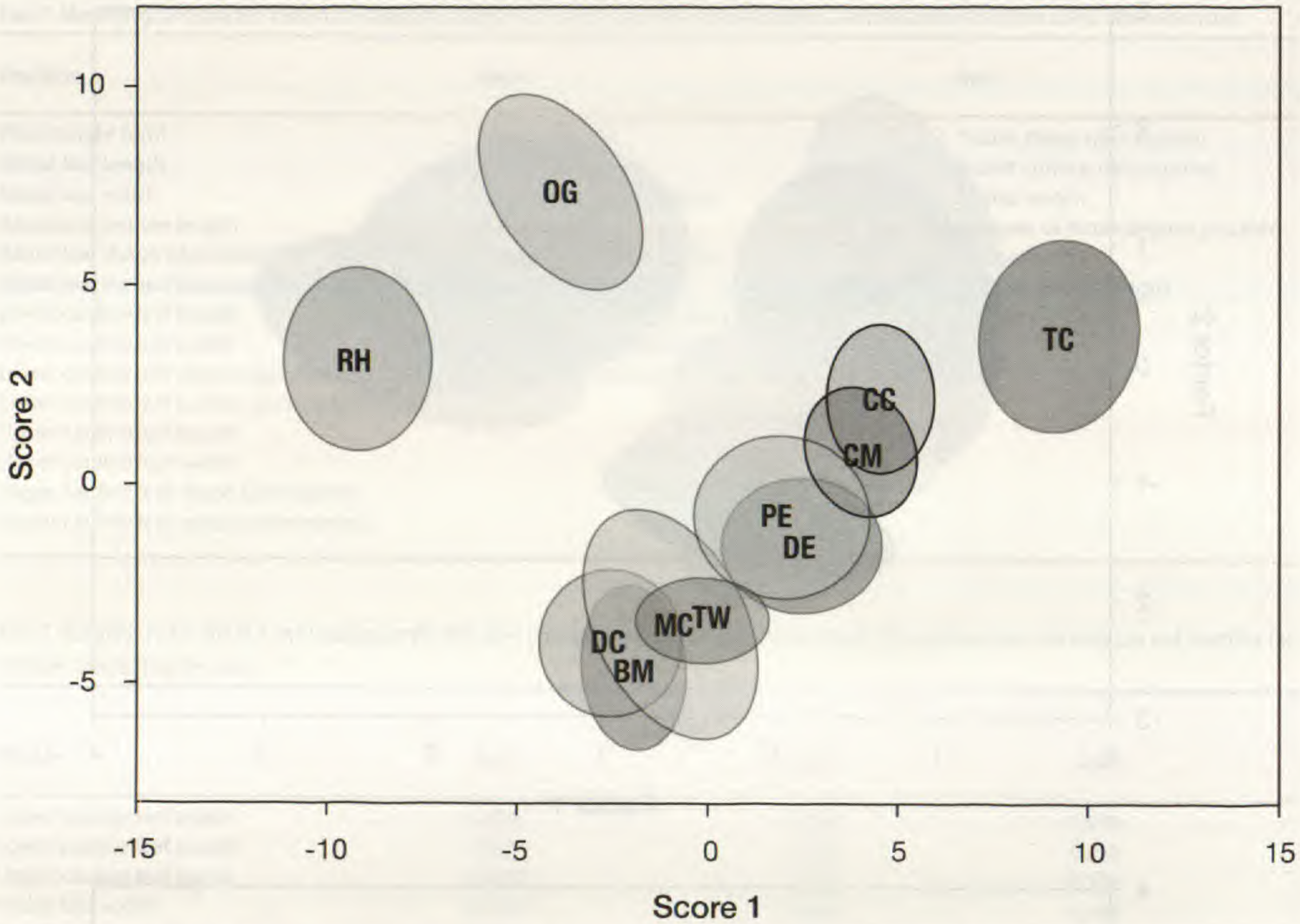

Fig. 3. Ordination of populations of *Hackelia* examined in this study based on two most discriminating functions. Functions 1 and 2 accounted for 81.8 % of the ability to distinguish among populations (51.2% and 30.6%, respectively). *Hackelia taylori* populations (CC and CM) are highlighted with heavy black line. *H. diffusa* var. *arida*: BM = Burch Mountain, TW = Tumwater Canyon, SC = Swakane Canyon, PE = Ponderosa Estates, MC = Moses Coulee, DE = Derby Canyon, DC = Douglas Creek. *H. diffusa* var. *diffusa*: OG = Oneota Gorge. *H. diffusa* var. *cottonii*: RH = Rattlesnake Hills. *H. venusta*: TC = Tumwater Canyon. *H. taylori*: CM = Cashmere Mountain, CC = Crystal Creek.

Similar to *Hackelia venusta* (Piper) St. John in aspects of morphology and habit but distinct in its habitat of higher places; shorter stature (1–2 dm vs. 2–4 dm); blue corollas (vs. primarily white) with much narrower limbs (10.0–15.0 mm wide vs. 18.0–22.0 mm) and smaller fornices (appendage 0.8–1.0 mm high vs. 1.0–1.4 mm; protuberance 0.6–1.0 mm long vs. 1.2–1.8 mm).

Moderately short perennial, 1–2 dm tall; stems often many from a slender taproot, erect or spreading from branched caudex. Leaves ciliate, antrorsely appressed strigose (Fig. 4A); radical leaves 3.7–10.4 cm long, 0.8–2.9 cm wide, linear-elliptical, appressed strigose, petiolate for 1/3 to 1/2 their length; cauline leaves linear to linear-lanceolate, sessile; lowermost cauline leaves 0.6–3.1 cm long, 0.4–1.2 cm wide; upper cauline leaves 1.9–5.3 cm long, 0.5–1.3 cm wide, reducing upward to the inflorescence, becoming small bracts. Pedicel 2.3–5.1 mm in flower (Fig. 3B) and 5.0-7.0 mm in fruit. Calyx length 2.4–3.4 mm, linear-lanceolate, strigose. Corolla limb blue, 1.0–1.7 cm wide with five lobes, lobes 3.0-5.0 mm long (Fig. 4D, F). Fornices with appendages showy, white, sometimes tinged pink, slightly emarginate, papillate-pubescent, rising 0.8–1.0 mm above the throat; protuberances yellow, pandurate, 0.6–1.0 mm long (Fig. 4D, E). Anthers 0.8–1.0 mm long. Nutlets 1.8–3.6 mm long, lanceolate-ovate; dorsal surface verrucose-hispidulous, intramarginal prickles 7–13; marginal prickles connate for up to 1/2 their length, forming a flange 1.2–2.4 mm wide around the nutlet; distinct prickle length 0.7–1.4 mm, a long prickle alternating with one or two shorter ones (Fig. 4C).

Etymology.—The epithet "*taylori*" honors Dr. Ronald J. Taylor, who taught botany at Western Washington University, Bellingham, Washington. Dr. Taylor co-authored the first status report for *H. venusta* in 1979 and was actively involved in native plant conservation in the Pacific Northwest for nearly 40 years.

TABLE 3. Variables used in the discriminant analysis and their relative usefulness in discrimination among populations. The asterisk reflects the top four values for each function that contributed most toward separation of *Hackelia* populations.

Variables	Function Coefficients		
	Function 1	Function 2	Function 3
Lower cauline leaf width	0.904*	-0.029	-0.039
Flange width (fruit)	0.502*	-0.415*	-0.460*
Calyx length (floral)	0.410*	0.094	-0.277
Fornice appendage (fruit)	0.404*	0.419*	-0.023
Limb width (floral)	0.271*	0.211	0.635*
Fornice protuberance (fruit)	0.245	-0.074	0.425*
Fraction connate (fruit)	0.163	-0.099	-0.198
Upper cauline leaf width	0.042	0.298	-0.277
Radial leaf width	0.014	0.082	-0.279
Anther length (floral)	0.007	0.014	-0.002
Upper cauline leaf length	-0.015	-0.446*	0.409
Radial leaf length	-0.046	-0.138	-0.025
Lower cauline leaf width	-0.063	0.427*	-0.121
# of intramarginal prickles (fruit)	-0.064	0.067	-0.014
Pedicel length (floral)	-0.088	-0.110	0.140
Nutlet length (fruit)	-0.192	-0.118	0.457*
Plant height	-0.231	-0.146	0.254
Lower cauline leaf length	-0.264	0.210	0.154
Distinct prickle length (fruit)	-0.323	0.332	-0.230
Radial leaf petiole length	-0.358	0.021	0.115

Hackelia taylori can be found growing on very steep, sandy/gravelly talus slopes within the Alpine Lakes Wilderness, Okanogan-Wenatchee National Forest at elevations, 1800-2300 meters. Only four populations are known: within the upper reaches of the Crystal Creek drainage, near Aasgard Pass, on the east slopes of Cashmere Mountain, and on the south slopes of Big Jim Mountain. Plants flower in late July and early August, producing seed within about two weeks of the initial flower.

DISCUSSION

Data collected for this study combined with data from Harrod et al. (1999) suggest that the high populations of *H. venusta* do represent a new taxon here recognized at the rank of species, and here named *H. taylori*. Reasons for species level recognition include distinct morphological differences, particularly flower color, markedly different habitats (Gamon 1988), absence of natural intermediate forms, lack of seeds produced in controlled crosses (Harrod, unpubl. data), and consistency with previous morphometric taxonomy in the genus (Gentry & Carr 1976). As in the current study, Harrod et al. (1999) found the high elevations populations of *H. venusta* were morphologically distinct from the low elevation population and sympatric populations of *H. diffusa* var. *arida*. In addition to flower color, they found that high elevations populations of *H. venusta* were distinct from the low elevation population with consistently smaller floral measurements, shorter stature, and wider and shorter radical and lower cauline leaves. Findings from the current study were similar in that *H. taylori* is not only morphological distinct from *H. venusta* (*sensu stricto*) but also from the complex of *H. diffusa*. Based on both principal components and discriminant function ordinations, *H. taylori* did not show morphological affinities with *H. diffusa* var. *diffusa* nor *H. diffusa* var. *cottonii*. These species are nearly four times taller, have larger leaves, and slightly larger fruits than *H. taylori*, and are always white flowered rather than blue.

The similar genetic identities described by Hipkins et al. (2003) suggest that *H. venusta* and *H. taylori* are closely related and may have diverged recently. The morphometric analysis may support recent divergence as well. Although forming distinct groups, *H. taylori* populations did slightly overlap the *H. venusta* population in the principal components ordination space when only the first two components are considered. The populations become clearly distinct with the third principal component, in which important floral (limb width and calyx length) and fruit (fornice protuberance and appendage) characters lead to separation. In addition, *H.*

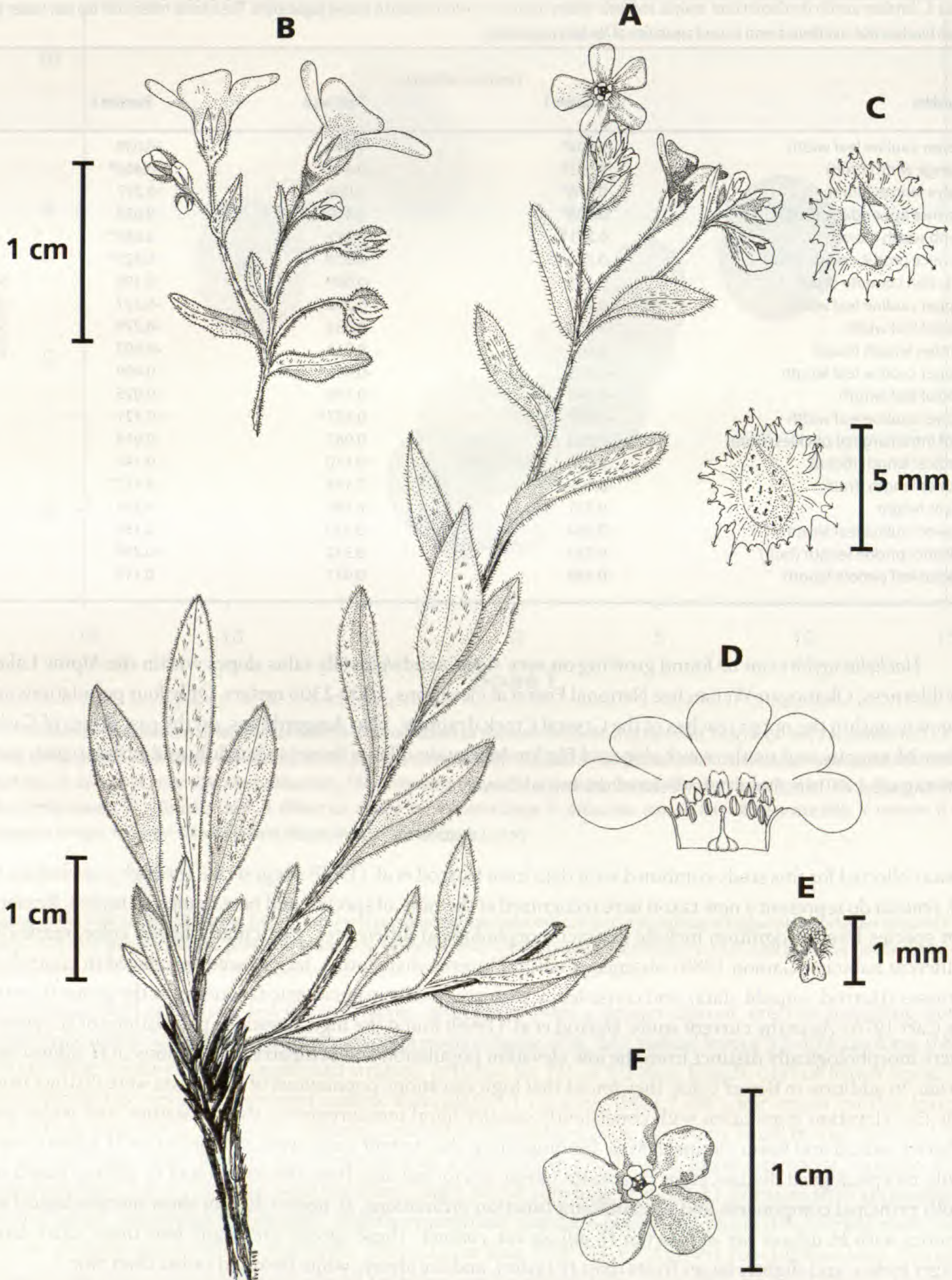

Fig. 4. *Hackelia taylori*. **A.** Plant with flowers and leaves; **B.** Inflorescence; **C.** Nutlets, upper view is ventral view, lower is dorsal view; **D.** Longitudinal section view of the corolla; **E.** Fornice; **F.** Top view of corolla. Bar = 1 cm in A, B, D, and F, and 1 mm in C and E.

taylori flowers are always blue and *H. venusta* flowers are white but sometimes tinged blue suggesting perhaps they share some genes for color.

Like *H. venusta,* this new species would benefit from well-developed conservation strategies. Populations are at risk from loss due to stochastic events, such as rock slides, which were the cause of the loss of most of one known population of *H. taylori*. Conservation strategies might include long-term seed banking so that populations could be re-established in the event of a stochastic loss.

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